A Quantitative and Qualitative Reanalysis of the Endocast From the Juvenile *Paranthropus* Specimen L338y-6 From Omo, Ethiopia

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KEY WORDS robust australopithecines; occipital sinus; cerebellum; *Parenthropus*

ABSTRACT Based on an analysis of its endocast, Holloway (1981 Am J Phys Anthropol *53*:109–118) attributed the juvenile Omo L338y-6 specimen to *Australopithecus africanus* (i.e., gracile australopithecines) rather than to *Paranthropus (Australopithecus) boisei* (robust australopithecines) favored by other workers (Rak and Howell [1978] Am J Phys Anthropol *48*:345–366). Holloway's attribution was based on the specimen's (1) low cranial capacity, (2) gracile-like meningeal vessels, (3) gracile-like cerebellar hemispheres, and (4) absence of an enlarged occipital/marginal (O/M) sinus system. Recent work, however, has shown that criteria 1 and 2 are not useful for sorting gracile from robust australopithecines (Culotta [1999] Science 284:1109–1111; Falk [1993] Am J Phys Anthropol *92*:81–98). In this paper, we test criterion 3 by quantifying the endocranial cerebellar and occipital morphology reproduced on the Omo L338y-6 endocast, and comparing it to seven endocasts from South and East African early hominids. Our preliminary results show that metric analysis of this specimen cannot be used to sort it preferentially with either robust or gracile australopithecines. Finally, we demonstrate that, contrary to previous reports, the Omo L338y-6 endocast reproduces an enlarged left occipital sinus (criterion 4). This observation is consistent with the original attribution of the Omo specimen to robust australopithecines (Rak and Howell [1978] Am J Phys Anthropol *48*:345–366). Furthermore, if Omo L338y-6 was a robust australopithecine, this discovery extends the occurrence of an enlarged O/M sinus system to one of the earliest known paranthropines. Am J Phys Anthropol 110:399–406, 1999.
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The cranial fragments (two relatively complete parietal bones, an almost complete occipital bone, and one small fragment of the left lateral frontal bone) of the juvenile hominid L338y-6 from Member E, Shungura Formation, Omo, Ethiopia were first described in detail by Rak and Howell in 1978. This specimen, dated to approximately 2.39 million years BP (Feibel et al., 1989), was estimated to have been a juvenile aged 10–12 years at death, partly because of the lack of spheno-occipital synchondrosal fusion in the cranium (Rak and Howell, 1978). Rak and Howell's (1978) age estimation of Omo L338y-6 was derived by interpolating between the estimated ages of Taung and OH 5, which at the time were 6.5 $\pm$ 1 and 15–17 years at death, respectively (Rak and

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Howell, 1978). Since 1978, reanalysis of dental eruption patterns and the microstructure of tooth enamel has shown that australopithecines tend to fit a great ape dental age scale more closely than a human dental age scale. Based on these data, Taung is estimated to have been around 3.3 and OH 5 11.3 years at death (Bromage and Dean, 1985; Bromage, 1987). Interpolating between these reevaluated ages at death, we estimate Omo L338y-6 to have been between 7–8 as opposed to 10–12 years at death.

Rak and Howell (1978) classified Omo L338y-6 as *Australopithecus (Paranthropus) boisei* based on the heavily incised inferior temporal and superior nuchal lines and the roughness of the planum nuchale in this young individual. Holloway (1981), on the other hand, interpreted the reconstructed endocast from this specimen as representing a gracile australopithecine (*Australopithecus africanus*) for four reasons: (1) the determined cranial capacity of 427 cm^3 was believed to be too low to be considered *A. (P.) boisei*, (2) the meningeal vessel pattern was said to resemble that of gracile rather than robust australopithecines, (3) the form of the cerebellar hemispheres was regarded as more gracile australopithecine-like, and (4) the specimen was said to lack an enlarged "accessory" occipital / marginal (O/M) venous sinus system that typifies robust australopithecines (Falk, 1986; Falk et al., 1995). Although Holloway later concluded that Omo L338y-6 was "perhaps indeed a 'robust' australopithecine (Holloway, 1988, p. 99)," he remained uncertain that it represented *A. (P.) boisei*, instead stressing its similarity with the well preserved KNM-WT 17000 specimen, that is classified as *A. (P.) aethiopicus* by some researchers (Kimbel et al., 1988). In this paper, we attempt to clarify further the taxonomic status of Omo L338y-6 by addressing the four traits listed above.

MATERIALS AND METHODS

The hominid paleoneurological record provides an incomplete picture of the occipital and cerebellar morphology of robust and gracile australopithecines. In an effort to assess the cerebellar morphology reproduced on the Omo L338y-6 endocast, we obtained seven measurements described below from its unreconstructed portions, and comparable measurements from unreconstructed parts of endocasts of four robust australopithecines (SK 1585, OH 5, KMN-ER 23000, KNM-WT 17000) and three gracile australopithecines (Sts 5, Sts 19, Taung). Measurements were taken from a partial occipital endocast of Omo L338y-6 kindly provided by Alan Walker. The metric and morphological accuracy of our partial endocast was verified by comparing its measurements with those from a complete endocast of the Omo L338y-6 specimen (endocast A, reconstructed by Ralph Holloway) at the American Museum of Natural History (New York), and two casts of the Omo L338y-6 cranial bones housed at the Musée de l'Homme (Paris), and the American Museum of Natural History. Endocasts from robust specimen KNM-ER 407 and the gracile specimen MLD 1 were also consulted for comparative morphological information only. The cranial capacities reported for each specimen are from Falk et al. (1999). Finally, we observed and measured a previously unrecognized occipital sinus on both endocasts of the Omo L338y-6 specimen. An illustration of this occipital morphology was obtained by digitally scanning our copy of the Omo specimen.

Measurements

1 and 2. Projected heights of the left and right cerebellar hemispheres, occipital view (PrH-L, PrH-R). Each endocast was oriented so that a line projecting through the frontal and occipital poles was parallel with a level surface (Fig. 1). Endocasts were then secured with cushions to allow easy access to the caudal (inferior) surfaces of the cerebellar hemispheres. Next, points CV (the most superior point on the cerebellar hemisphere inferior to the transverse sinus) and CI (the most inferior point on the cerebellar hemisphere) were determined from occipital views of each endocast, and the projected distance between these points measured with a sliding caliper furnished with sliding prongs. When fossil material was complete enough, these procedures were repeated independently for each cerebellar hemisphere.

3 and 4. Chord heights of the left and right cerebellar hemispheres, occipital view (ChH-L, ChH-R). Endocasts were oriented and secured as described for measurements 1 and 2, and a sliding caliper was

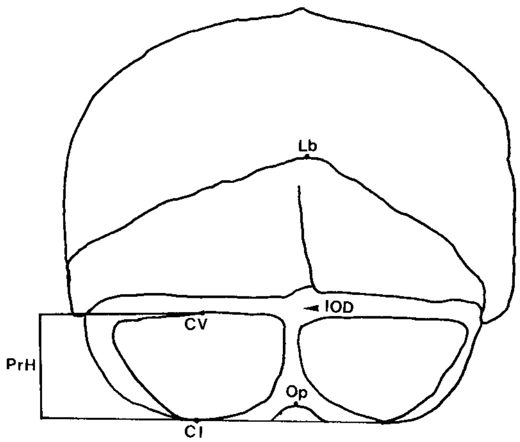

Fig. 1. Human endocast in norma occipitalis. CI = the most inferior point on the cerebellum in norma occipitalis, CV = the most superior point of the cerebellum in norma occipitalis, IOD = internal occipital depression (corresponding to the internal occipital protuberance), Lb = lambda, Op = opisthion, PrH = projected cerebellar height (redrawn from Connolly 1950, pp. 316).

used to measure the chord distance between points CV and CI. This chord was taken on both cerebellar hemispheres where feasible.

5. Lambda-internal occipital depression (Lb-IOD). Lb (the point at which the lambdoid and sagittal sutures meet) and IOD (the center of the depression on the endocast that corresponds to the internal occipital protuberance) were located and marked on the endocranial casts. Sliding calipers were then used to obtain the chord measurements between these two points.

6. Internal occipital depression-opisthion (IOD-Op). As described above, IOD and Op (the point corresponding to the midline point on the posterior border of the foramen magnum) were located and marked on each endocast, and sliding calipers used to obtain the chord measurements.

7. Cranial capacity in cubic centimeters (CranCap). All cranial capacities, some of which are revisions of earlier estimates, were taken from the literature (Falk et al., 1999).

RESULTS

Trait 1: cranial capacity

Because previously unknown portions of robust australopithecine endocasts have become available since a number of endocasts were first reconstructed, endocasts have recently been re-reconstructed for four robust australopithecines specimens, and new cranial capacities determined for these latest reconstructions (Falk et al., 1999). The new cranial capacities for robust australopithecines are lower than earlier estimates and the new mean of 450 cm^3 for eight specimens is significantly ($p < .05$, two-tailed) lower than the currently accepted mean of 492 cm^3 (Falk et al., 1999). However, the new mean does not differ significantly from that of 451 cm^3 for gracile australopithecines, which contradicts the commonly held view that robust australopithecines, on average, had significantly larger brains than gracile australopithecines (Falk et al., 1999). Since mean cranial capacity is indistinguishable between robust and gracile australopithecines, this trait cannot be used to assess the taxonomic status of Omo L338y-6.

Trait 2: meningeal vessels

The assertion that the meningeal vessel pattern on the Omo L338y-6 endocast sorts it with gracile rather than robust australopithecines was based on an analysis (Saban, 1985) that utilized Adachi's (1928) system for scoring human middle meningeal branching patterns. A relatively recent comparative study on meningeal patterns in great apes (Falk, 1993), however, shows that Adachi's system is inappropriate for assessing meningeal patterns in nonhuman primates and early hominids. For reasons detailed elsewhere (Falk, 1993), the meningeal vascular pattern on the Omo endocast cannot be used to sort it with either genus of australopithecine.

Trait 3: cerebellar hemispheres

Table 1 provides measurements obtained from the cerebellar and occipital regions of endocasts from gracile and robust australopithecines. The left and right cerebellar heights, projected (PrH-L, PrH-R) and chord (ChH-L, ChH-R), were averaged for each specimen and the resulting averages used to determine the means for the two types of australopithecines. The projected heights average 20.8 mm for gracile specimens Sts 5 and Sts 19 and $\geq$ 25.6 mm for robust speci-

TABLE 1. Robust and gracile Australopithecine endocranial cast measurements[1]

	Sts 5	Sts 19	Taung	OH 5	KNM-ER 23000	SK 1585	KNM-WT 17000	Omo L338y-6
1. PrH-L	—	18	—	27	≥23	—	—	—
2. PrH-R	23.5	—	—	26.5	—	27	—	≥25
3. ChH-L	—	32	—	31	26	—	—	—
4. ChH-R	29	—	30	31	—	35	—	≥28
5. Lb to IOD	34.5	—	—	23	30	29.5	—	34
6. IOD to OP	15	20	—	27	—	—	—	23.5
7. CranCap	485	436	440	500	491	476	410	427

[1] 1–6 measured in mm and 7 in cm^3.

mens OH 5, KNM-ER 23000, and SK 1585. The measurement for Omo L338y-6 of ≥ 25 falls above the gracile mean and near the robust mean, although the two groups do not differ statistically for this trait (two-tailed Student's t-test $p < .05$). Thus, despite its small estimated cranial capacity, the Omo specimen is closer to robust australopithecines on the absolute size of this feature. (Furthermore, the measurements on the Omo specimen are minimal estimates because the specimen is broken where the base of the cerebellar hemispheres begin.)

Because the mean chord height of 30.3 mm for the three gracile specimens does not differ significantly from that of 30.7 mm for the three robust specimens, the ≥ 28 mm measurement for Omo L338y-6 does not appear to sort with either type of australopithecine. Measurements 5 and 6 were performed to assess the relative position of the cerebellar hemispheres in relation to Lb and Op, since Tobias (1967) reported that the internal occipital protuberance (IOD on the endocast) of OH 5 migrated toward Lb demonstrating a rostro-caudal expansion of the cerebellum similar to modern humans. In fact, the 34 mm Lb-IOD measurement on the Omo endocast is not significantly greater than the mean of 27.5 mm for three robust endocasts (which happen to have greater volumes) and nearly identical to that on the Sts 5 endocast (which also has a greater volume than the Omo specimen). It therefore appears that IOD has not migrated towards Lb in this specimen. Similarly, the data collected for IOD-Op do not align the Omo endocast with either genus of australopithecine. Together, these data show that the above measurements cannot be used to assess the taxonomic status of the Omo L338y-6 specimen.

Trait 4: occipital/marginal sinus

A number of workers have stated that the Omo L338y-6 specimen does not possess an enlarged O/M venous sinus system (Holloway, 1981; Kimbel, 1984; Rak and Howell,1978). Contrary to these reports, we observe the superior portion of a left occipital sinus in Omo L338y-6 (Fig. 2). The widest portion of the left occipital sinus is 4 mm superior to the broken lower edge of the partial endocast and measures between 4 and 5 mm transversely. The caliber of the occipital sinus is similar to the previously detected right transverse sinus. The right margin of the occipital sinus angles superiorly toward the confluence of the sinuses and then curves laterally toward the left transverse sinus. The left margin of the occipital sinus partially obscures the medial edge of the left cerebellar hemisphere. In their analysis of the Omo L338y-6 cranial remains, Rak and Howell (1978) characterized the medial border of the right cerebellar fossa as well defined, but described the medial border of the left cerebellar fossa as much less obvious, flowing into the fossa more continuously. Their published diagram of the endocranial aspect of the Omo L338y-6 occipital bone (Rak and Howell, 1978:356) includes stippling which is continuous with the left transverse sinus and that, we believe, corresponds to the left occipital sinus. A hairline crack runs supero-inferiorly along the medial margin of the left occipital sinus away from the left cerebral fossa. This crack is almost seamless and in no way obscures the left occipital sinus groove. As discussed below, of the four traits we have explored, the observation of a distinct occipital sinus may have implications for the taxonomic classification of Omo L338y-6.

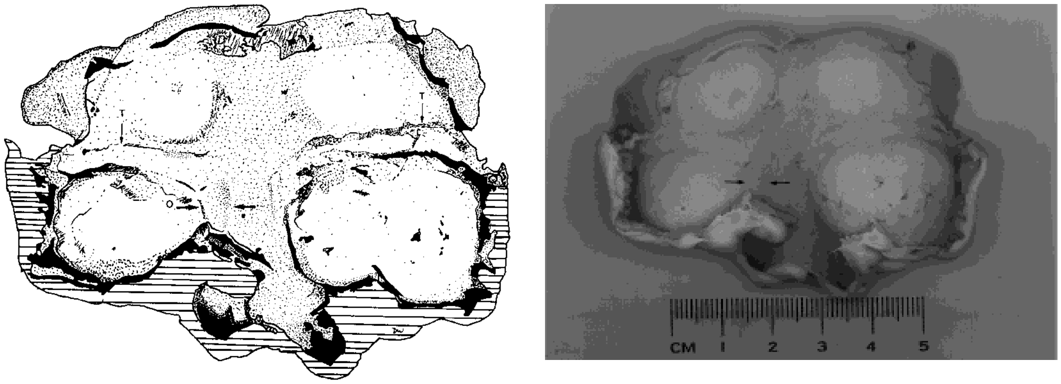

Fig. 2. Occipital illustration of Omo L338y-6 partial endocast (left). T = transverse sinuses, O = occipital sinus. Scanned photographic image of Omo L338y-6 partial endocast (right). The arrows demonstrate the location of the occipital sinus (scale in cm).

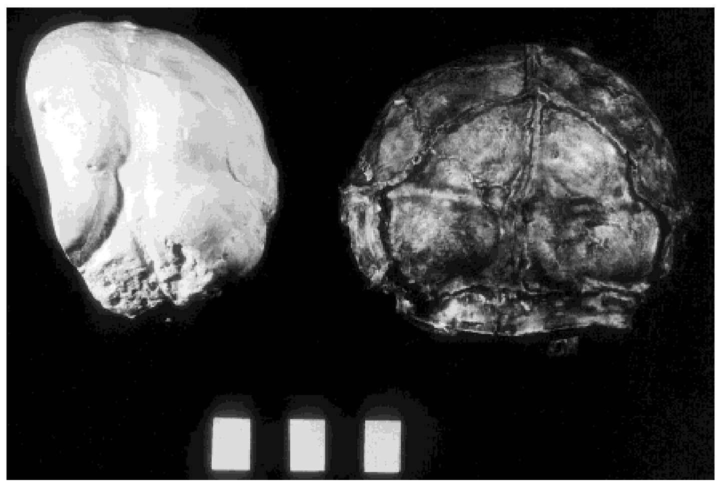

Fig. 3. SK 1585 (left) and KNM-ER 23000 (right) in norma occipitalis (scale in cm).

Other observations

The inter-cerebellar region. The left cerebellar hemisphere of Omo L338y-6 is not as pronounced as the right and forms a more continuous surface with the inter-cerebellar region, the endocranial equivalent of the vermal fossa (Rak and Howell, 1978). The region between the protruding occipital lobes and the cerebellar hemispheres contains the impression of the transverse venous sinuses. The confluence of the venous sinuses (which corresponds to the endocranial internal occipital depression), as well as the zone between the cerebellar hemispheres inferior to the confluence (which corresponds to the inferior sagittal limb of the cruciate eminence) are flat and wide in Omo L338y-6 (Fig. 2). The endocranial impression of the inferior sagittal limb of the cruciate eminence measures between 10–11 mm transversely from the lateral edge of the occipital sinus to the medial edge of the right cerebellar hemisphere. This wide gap between the cerebellar hemispheres is reminiscent of the corresponding area in OH 5, SK 1585, and KNM-ER 23000 (Fig. 3).

As Tobias (1967) and Rak and Howell (1978) suggested, the protruding cerebral lobes and wide flat vermal fossae may be used to differentiate between gracile and robust australopithecines (Fig. 3), i.e., that the internal occipital depression forms a pointed impression and is much sharper in gracile australopithecines and modern hu-

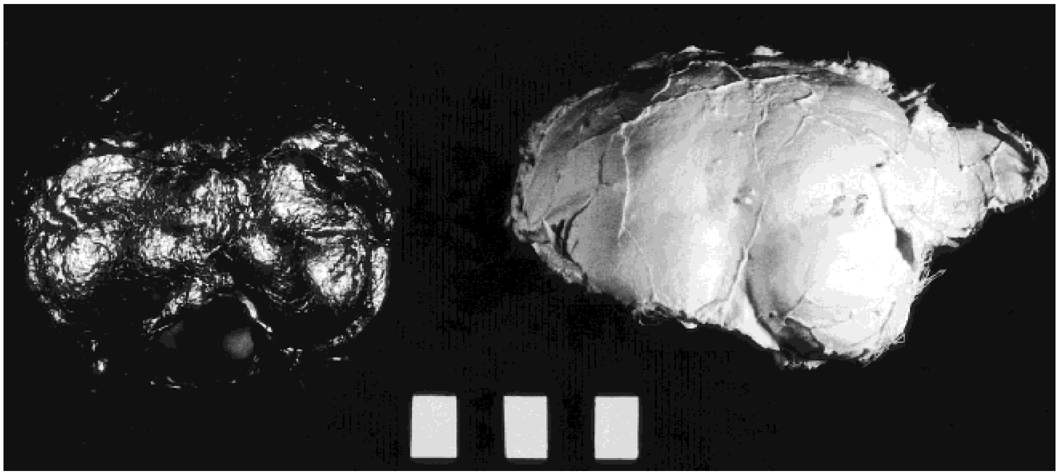

Fig. 4. Sts 5 (left) and MLD 1 (right) in norma occipitalis (scale in cm).

mans than in robust australopithecines. The inferior sagittal limb is also much narrower in gracile forms such as in MLD 1 and Sts 5 (Fig. 4). In this respect, Omo L338y-6 is very similar to OH 5, SK 1585, KNM-ER 23000 and KNM-ER 407 (Rak and Howell, 1978).

The sagittal and transverse sinuses. Rak and Howell (1978) noted that the superior sagittal sinus was difficult to trace on the endocranial surface of the Omo L338y-6 cranium and that it was also obscured on the endocast. They also stated that "...two grooves marking the route of the transverse sinuses are easily recognizable on the lateral limbs of the cruciate eminence" (Rak and Howell, 1978, p. 352). The widest portion of the left transverse sinus of our partial endocast is located just superior to the medial margin of the left cerebellar hemisphere and measures between 6–7 mm. The right transverse sinus is widest at the approximate midline of the right cerebellar hemisphere where it measures between 4–5 mm. The left transverse sinus protrudes further, is wider, and is longer than the right transverse sinus. Unfortunately, the specimen is damaged at the level of the sigmoid sinuses, which therefore cannot be detected.

DISCUSSION

Taxonomic inferences about Omo L338y-6

We can no longer assume that the mean cranial capacity of robust australopithecines is significantly larger than that of gracile australopithecines (Culotta, 1999; Falk et al., 1999). Thus, Hollway's (1981) first argument that the cranial capacity of Omo L338y-6 at 427 cm^3 was too low to be considered a member of *Paranthropus* is unsupported. Secondly, Saban's (1985) system of scoring meningeal vessels based on Adachi (1928) is now known to be inappropriate for assessing the meningeal vessel pattern of early hominids (Falk, 1993) and is therefore not useful for sorting robust from gracile australopithecines. Thirdly, our quantification of the occipital and cerebellar morphology on the endocast from Omo L338y-6, and comparison with similar measurements on unreconstructed parts of endocasts from *Paranthropus* and *Australopithecus* have proven (possibly because of small sample sizes) to be ineffective in shedding light on the taxonomic affinity of the former.

Lastly, as we have demonstrated above, the Omo L338y-6 endocast reproduces an enlarged occipital sinus running along the left cerebellar hemisphere complimenting the two transverse sinuses. Interestingly, a similar reevaluation of the occipital and marginal sinus system of the Taung specimen was reported by Tobias and Falk (1988). In the case of Taung, the right occipital and marginal sinus impressions termed "unmistakable" by Tobias and Falk (1988), went unnoticed for almost 65 years of intensive investigation of this specimen. This apomor-

phic character is found in all scorable robust australopithecines, both *Paranthropus robustus* and *Paranthropus boisei* (but see Suwa et al., 1997, discussed below), and all scorable *Australopithecus afarensis* specimens from Hadar. An enlarged O/M sinus has been observed in only one *Australopithecus africanus* specimen, the type specimen Taung (Falk and Conroy, 1983; Falk, 1986; Falk et al., 1995; Kimbel et al., 1982; Kimbel et al., 1994; Brown et al., 1993). It is important to note, however, that Taung possesses a number of other characteristics that typify robust rather than gracile australopithecines (Tobias, 1973; 1974; Olson, 1974; Tobias and Falk, 1988; Conroy and Vannier, 1987; White, 1996).

Recently, Suwa et al. (1997) described a newly discovered 1.4 million year old *Paranthropus boisei* from Konso, Ethiopia which was scored as having "no trace of either occipital or marginal sinuses, although impressions for the transverse sinuses are also lacking" (Suwa et al., 1997, p. 491). The authors added that "(n)evertheless, a bilaterally developed sigmoid sinus groove suggests that venous drainage was by the transverse-sigmoid route." In a personal communication to DF, Suwa noted that "the absence of the O/M is based on the unilaterally preserved relevant portion (preservation extends from the cruciate eminence area to a small segment of the foramen magnum)."

A lateral transverse-sigmoid sinus drainage system sometimes coexists with an enlarged O/M sinus system in modern and fossil hominids, and the presence of an enlarged bilateral sigmoid sinus system does not preclude the presence of an enlarged O/M system (Falk, 1986; Kimbel 1984, Tobias and Falk, 1988). It is therefore impossible to know for certain whether an O/M sinus system was present on the unpreserved side of the Konso specimen, as is the case with Sts 71 (Tobias and Falk, 1988). Furthermore, (Tobias and Falk, 1988, p. 312) "a study of a large number of ancient and modern hominids suggests that the lack of transverse sinus grooves in a fragmentary specimen *does* provide indirect evidence that an enlarged occipital-marginal sinus system would probably have been present (as in OH 5, ER 407, and Guomde)." Thus it is entirely possible that the *Paranthropus boisei* from Konso, Ethiopia, had an enlarged unilateral O/M sinus system.

CONCLUSION

The massive sagittal and nuchal crests, the overlapping and striated squamosal sutures, the heart-shaped foramen magnum, the deep protrusion of the occipital poles inferior to the lambdoid suture, the wide flat inter-cerebellar region (Tobias, 1967; Rak and Howell, 1978; Walker and Leakey, 1988) and now, the presence of an enlarged occipital sinus, all point to the robust australopithecine status of Omo L338y-6. The existence of an occipital venous sinus in Omo L338y-6 demonstrates that at approximately 2.4 million years BP, whether it is classified *Paranthropus boisei* or *Paranthropus aethiopicus*, this specimen shared a derived enlarged O/M sinus with earlier 3–4 million year old hominids from Ethiopia (*Australopithecus afarensis*) and later 2.2–1.4 million year old *Paranthropus boisei* and *Paranthropus robustus* specimens from East and South Africa.

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LITERATURE CITED

Adachi B. 1928. Das arteriensystem der japaner. band 1. Kyoto:Verlag Der Kaiserlich-Japanischen Universitat Zu Kyoto.

Bromage TG. 1987. The biological and chronological maturation of early hominids. J Hum Evol 16:257–272.

Bromage TG, Dean MC. 1985. Re-evaluation of the age at death of Plio-Pleistocene fossil hominids. Nature 317:525–528.

Brown B, Walker A, Ward CV, Leakey RE. 1993. New *Australopithecus boisei* calvaria from East Lake Turkana, Kenya. Am J Phys Anthropol 91:137–159.

Conroy G, Vannier MW. 1987. Dental development of the Taung skull from computerized tomography. Nature 329:625–627.
Culotta E. 1999. Anthropologists probe bones, stones, and molecules. Science 284:1109–1111.
Falk D. 1986. Evolution of cranial blood drainage in hominids: Enlarged occipital/marginal sinuses and emissary foramina. Am J Phys Anthropol 70:311–324.
Falk D. 1993. Meningeal arterial patterns in great apes: Implications for Hominid vascular evolution. Am J Phys Anthropol 92:81–98.
Falk D, Conroy G. 1983. The cranial venous sinus system in *Australopithecus afarensis*. Nature 306:779–781.
Falk D, Gage TB, Dudek B. 1995. Did more than one species of hominid coexist before 3.0 Ma?: Evidence from blood and teeth. J Hum Evol 29:591–600.
Falk D, Guyer J, Redmond JC, Conroy GC, Recheis W, Weber GW, Seidler H. 1999. Early hominid brain evolution: a new look at old endocasts. (in review)
Feibel CS, Brown FH, McDougall I. 1989. Stratigraphic context of the fossil hominids from the Omo group deposits: northern Turkana basin, Kenya and Ethiopia. Am J Phys Anthropol 78(4):595–622.
Holloway RL. 1981. The endocast of the Omo L338y-6 juvenile hominid: "Gracile" or "robust" *Australopithecus*? Am J Phys Anthropol 53:109–118.
Holloway RL. 1988. "Robust" australopithecine brain endocasts: some preliminary observations. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 247–258.
Kimbel WH. 1984. Variation in the pattern of cranial venous sinuses and hominid phylogeny. Am J Phys Anthropol 63:243–263.
Kimbel WH, Johanson DC, Coppens Y. 1982. Pliocene hominid cranial remains from the Hadar Formation, Ethiopia. Am J Phys Anthropol 57:403–452.
Kimbel WH, White TD, Johanson DC. 1988. Implications of KNM-WT 17000 for the evolution of "robust" *Australopithecus*. In Grine FE, editor. Evolutionary History of the "Robust" Australopithecines. New York. Aldine de Gruyter, pp. 259–268.
Kimbel WH, Johanson DC, Rak Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. Nature 368:449–451.
Rak Y, Howell FC. 1978. Cranium of a juvenile *Australopithecus boisei* from the Lower Omo Basin, Ethiopia. Am J Phys Anthropol 48:345–366.
Saban R. 1985. Identification des stades evolutifs des hommes fossiles d'apres les veines meningees. Actual Odonto-stomatol 152:693–712.
Suwa G, Berhane A, Beyene Y, White TD, Katah S, Nagaoka S, Nakaya H, Uzawa K, Renne P, WoldeGabriel G. 1997. The first skull of *Australopithecus boisei*. Nature 389:489–492.
Tobias PV. 1967. The cranium and maxillary dentition of *Australopithecus (Zinjanthropus) boisei*. Olduvai Gorge, Vol. 2. Cambridge: Cambridge University Press.
Tobias PV, Falk D. 1988. Evidence for a dual pattern of cranial venous sinuses on the endocranial cast of Taung (*Australopithecus africanus*). Am J Phys Anthropol 76:309–312.
Walker AC, Leakey RE. 1988. The evolution of *Australopithecus boisei*. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 247–258.
White DD. 1996. Implications of cerebellar morphology on the classification of enigmatic fossil hominids (abstract). Am J Phys Anthropol 22(Suppl):242.